

The courtship behavior of *Callophrys xami* (Lycaenidae)

Carlos Cordero

Centro de Ecología, Universidad Nacional Autónoma de México, Apdo. Post. 70-275, Delegación Coyoacán, 04510 D. F., México.

Abstract. The courtship behavior of the butterfly *Callophrys xami* (Lycaenidae) was studied in the field. The typical courtship pattern as well as behavioral variants are described and discussed in terms of mate choice and variation in female receptivity. Copulatory behavior leading to separation of the pair well before the time necessary for successful mating (less than three minutes vs. 32 minutes) is described. The possible role of this last behavior in mate choice is discussed.

KEY WORDS: Courtship, copulation, behavioral variation, mate choice

INTRODUCTION

Intraspecific variation in courtship behavior in butterflies is well documented and it has been explained as a result of mate choice by males and/or by females (e. g. Rutowski, 1979, 1981-83, 1984; Wiklund and Forsberg, 1985; Krebs, 1988). Furthermore, Eberhard (1985, 1994, in press; Eberhard and Cordero, 1995) proposes that in animals courtship may continue during copulation and that females can also use this *copulatory courtship* for their choice of mate. In this paper, variation in precopulatory courtship and behavior during copulation in *Callophrys xami* is reported, and some of its possible causes discussed.

METHODS

The study was conducted in an ecological preserve of 146.8 ha, located on the campus of the Universidad Nacional Autónoma de México, south of Mexico City. This area is part of the Pedregal de San Angel, a zone characterized by volcanic soil, rough topography, markedly seasonal rainfall regime, and xerophytic shrubby vegetation (Rojo, 1994).

Callophrys xami is a multivoltine butterfly that can be found throughout the year. The Pedregal de San Angel population never reaches a very high density of individuals and it is more abundant from October to January (Soberón *et al.*, 1988). The main food plant of the larvae is the perennial *Echeveria gibbiflora* (Crassulaceae), an abundant species in the area (Soberón *et al.*, 1988). Males are territorial, and a male can occupy the same territory for as long as four weeks (Cordero, 1996). Territories are areas with well defined topographical limits, located beside or on natural or man-made trails; these areas lack concentrations of receptive females and larval and adult food resources. Males actively defend their territories by means of different types of aggressive flights, for an average of five hours per day (approximately between 1000 and 1500 h), and spend the rest of the time feeding and resting outside territories (Cordero and Soberón, 1990). Territories function as mating stations (Cordero and Soberón, 1990; Cordero, 1996).

Observations were made in 1989, between November 1 and December 20, and in 1990, between November 10 and December 6. The number of territories observed was 19 in 1989 and 13 in 1990; the number of days a territory was visited varied between 29 and 38 in 1989 and between 14 and 24 in 1990 (details in Cordero, 1996). Most territorial males observed were captured and individually marked on the wings with indelible felt-tip pens (Sharpie®) that does not seem to have effects on males (Cordero and Soberón, 1990). Observations of courtships and copulations were made on groups of territories located on transects; we walked these transects at least two times per day during 31 days in 1989 and 11 days in 1990, making focal observations in each territory for at least three minutes after locating the resident male. Courtships and copulations were also observed during continuous observations of selected territories, made for 9 days in 1989 and for 13 days in 1990. Twelve courtships observed in 1983-1985 (during the course of another study; Cordero and Soberón, 1990) are included in the description of typical courtship.

RESULTS

Typical successful courtship

The following description is based in 20 complete successful courtships observed in the field. This typical pattern was observed in the 12 successful courtships observed in 1983-1985, in five out of the 10 observed in 1989, and in three of the five observed in 1990. The temporal sequence of courtship and mating can be divided in seven phases (Fig. 1):

I. A female flies near (< 1 m) a flying or, more frequently, a perching male.

II. The male flies following the female and a courtship flight along a route parallel to the ground begins; during the courtship flight the male flies near (< 10 cm), slightly behind and a few cm above the female. This flight lasts about 30 seconds, unless a perturbation, such as a strong wind, momentarily interrupts the courtship, in which case the flight lasts longer.

III. Female and male alight on vegetation close to each other; there were a few cases in which one or more alighting attempts preceded final settling of the pair.

IV. Immediately after the couple alight on vegetation, the male walks in front of the female until reaching a head to head position, while fluttering vigorously; meanwhile, the female stays motionless with her wings closed. It is possible that during this phase (and, probably, since phase II) the male emits pheromones from androconia located near the forewing costal border.

V. After a few seconds, and still fluttering, the male walks beside the female until reaching a parallel, head to head and tail to tail position.

VI. The male moves the tip of his abdomen toward that of the female and, after making genital contact, stops fluttering; immediately after beginning copulation the male moves until reaching the "tail to tail" copula position typical of Lepidoptera. During copulation the couple stays motionless, unless some perturbation, such as strong wind or people coming too close to the mating pair, makes them fly *in copulo* to a different place on vegetation. The approximated time elapsed between alighting and beginning of copulation (phases IV to VI) is between 10 and 20 seconds.

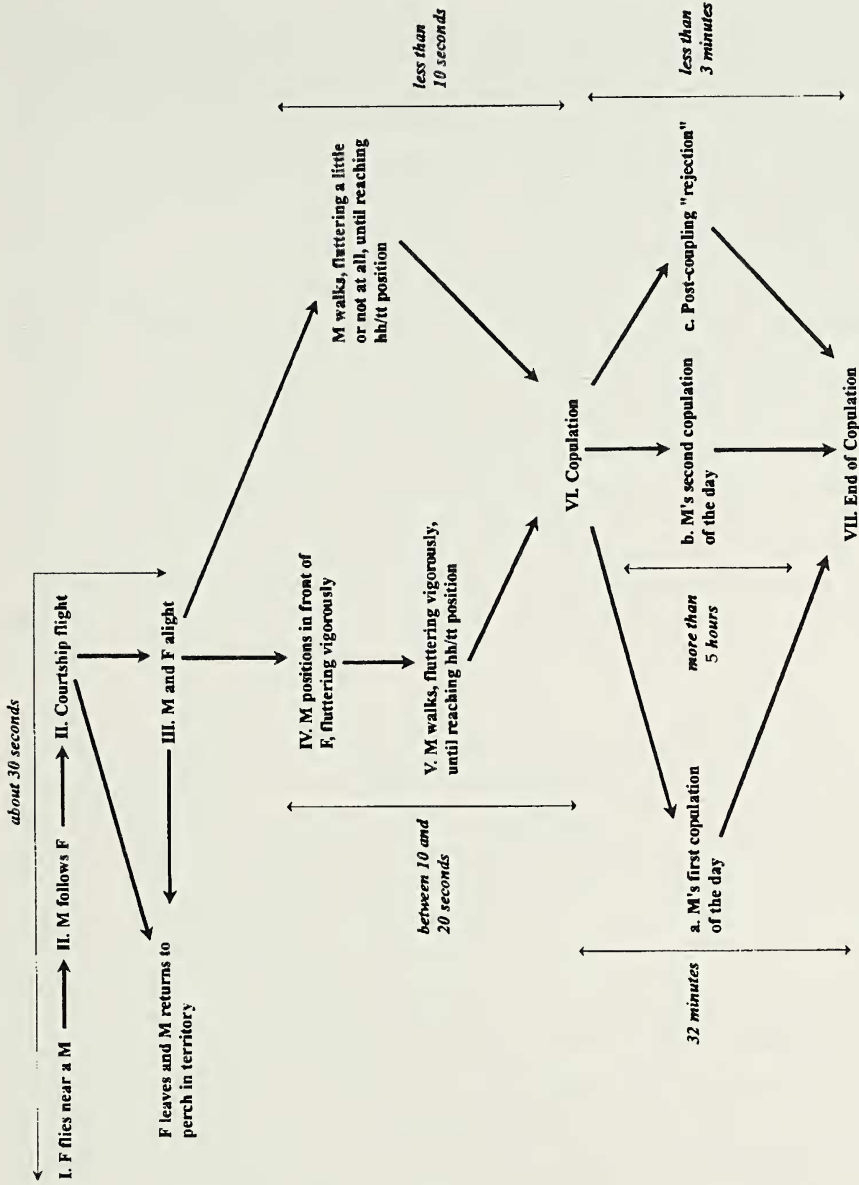


Fig. 1. Diagram of the mating behavior of *Callophrys xami* (Lycaenidae), showing variations in courtship and post-coupling behavior. Courtship description is based in 27 observations. M: male. F: female. hh/lt: M parallel to the F, head to head and tail to tail.

VII. The end of copulation begins with the female starting to move, turning and occasionally walking short distances (less than 20 cm); these movements are intercalated with female turnings around her longer body axis, until the pair ends genital contact. After separation the female and/or the male may remain in the mating place for a few minutes or they may fly away almost immediately. In few occasions the male found the female again, after seconds or a couple of minutes, and a short pursuit flight followed, which ended when the male returned to perch and the female left the area.

Courtship is mostly initiated inside territories, although the possibility exists that a female is found by a male when he is returning to his territory after, for example, an aggressive interaction. Copulations can take place inside territories, and they also occur outside, if the courtship flight takes the pair out of the territory. Average copulation duration in the field is 32.3 min (Standard Error = 4.9; Cordero, 1996); duration is much longer (range: 1h42 min to >14h; 23/24 copulations lasted > 5h) if the copulation is the second of the day for the male (Cordero, 1996). In captivity, courtship begins when a male detects a female at short distance, usually when the male and/or the female are walking on the cloth of the cylindrical, 58 cm high by 26 cm diameter, mating cages (Jiménez and Soberón, 1988-89); afterwards, courtship and mating proceeds from phase IV on, as in the field.

Courtship Variants

In five out of 10 successful courtships observed in 1989 and in two of the five observed in 1990, the time allocated to the vigorous fluttering (phases IV, V and part of VI) was considerably less than in the typical courtship described above, and in some cases it was almost absent (Fig. 1). This difference also occurred in some of the courtships observed in captivity.

We have observed several courtships in the field that did not result in mating. Several were observed in 1983-1985, 13 in 1989 and 29 in 1990. The duration of these unsuccessful courtships was variable, but observations lacked the detail necessary to look for differences between successful and unsuccessful courtships. These courtships lasted from a few seconds to rarely more than one minute. Almost all complete observations of unsuccessful courtships (some couples were lost from sight) ended before phase III, although at least in one case a male lost a female during alighting attempts (in this specific case, the strong wind blowing during observation, rather than mate choice [see discussion], may be responsible for the unsuccessful courtship).

Copula Interruption

In one of 17 copulations observed in 1989 and one of 10 observed in 1990, the female began walking after genital coupling began, dragging the male behind her. After a brief time, the female began to intercalate body twists during walking, behaving in the same way as when they are about to finish normal copulation (see phase VII of typical courtship), suggesting attempts to end copulation. Both cases resulted in the separation of the pair less than

three minutes after mating began (probably before ejaculate transfer and long before the end of normal copulations; Cordero, 1996).

In the case observed in 1989 the male encountered the female again, less than three minutes after separation, and courted her for a second time without success; afterwards the female left the area and the male returned to perch in the territory. The male had been defending the territory for at least five days before, and defended it three more days after; his minimum longevity was nine days (mean minimum longevity of males observed in 1989 more than one day = 6.9 days, s.e. = 0.8, range: 2-20, n = 51; Cordero, 1996); the forewing length (a measure of body size; Parlange, 1991; Cordero, 1996) of this male was 1.73 cm (mean forewing length of males observed in 1989 = 1.64 cm, s.e. = 0.01, range: 1.36-1.89 cm, n = 77; Cordero, 1996) and whether the male or the female had mated earlier the day of the interrupted copulation is unknown, given that we began observations in that territory at 1130. In the 1990 case the male had defended the territory at least one day before the "rejection" (his minimum longevity was four days); we did not measure the forewing length of this male. We do not know if the male or the female had mated earlier the day of the "rejection", given that we began observations after 1100. These two males were not observed mating for a second time.

We observed similar behavior in another two cases, one in the field and one in captivity, but these occurred after a perturbation. In the first case, the female exhibited the behavior after we attempted to put the field mating pair inside a cage; the time at which this mating began is unknown. The second case occurred when the mating cage accidentally fell to the ground more than five minutes after the mating had begun. We never observed this behavior in any of the 18 matings observed in 1983-1985.

DISCUSSION

Variation in successful courtships

Typical courtship behavior of *Callophrys xami* is similar to the courtship of related species (e. g. Powell, 1968; Robbins, 1978); however, to my knowledge, variation in this behavior has not been reported in other *Callophrys* species. Courtship variants may be the result of differences in female receptivity. Males finding highly receptive females may save time, energy and pheromones with the shortening of courtship phases IV to VI. Female receptivity may be affected by time since last mating, time since emergence from the pupa (this applies to virgin females of species able to mate and lay eggs almost immediately after emergence, such as *C. xami*), number of sperm remaining in her spermatheca, size and quality of the last ejaculate received (e. g. Oberhauser, 1992; Kaitala and Wiklund, 1994), remaining quantity of receptivity inhibition substances transferred by her last partner (Cordero, 1995), number of mature eggs stored, feeding condition (e. g. Boggs, 1990) and courting male quality (Thornhill and Alcock, 1983; Eberhard, in press; Cordero, 1995), among other factors.

In *C. xami* time since last mating is positively correlated with female receptivity (Cordero, 1996), but at this moment we do not know if time *per se* or other correlated factors (such as the quantity of some of the different ejaculate components remaining stored in the female) are responsible for differences in female receptivity. Males probably emit pheromones during phases IV to VI, and this also suggests that females involved in "short" courtships could have been highly receptive (and, therefore, in need of less stimulation). (A few observations suggest that at least some females come into actual or potential territories, flying within them in a way that could possibly make them very conspicuous to territorial males. If the function of this behavior is to make females easily detected by males, we expect to observe it only in receptive females.)

An alternative explanation for the "shortening" of courtships may be physical exhaustion of the male forcing him to reduce the possibly costly courtship phases IV to VI. However, our observations of the conditions of males, as well as the low frequency of male-male and male-female interactions reported in *C. xami* (Cordero and Soberón, 1990; Cordero, 1996), suggest that this second hypothesis is not a general explanation for these behavioral variants; besides, if this hypothesis is correct, we need to explain why females accepted these exhausted males. If we accept the idea that females gain information about male quality during courtship, a third hypothesis is that males involved in the "short" courtships could have been males of very high quality, quickly identified as such and accepted by females.

Mate choice and copula interruption

Although mate choice has not been studied in *C. xami*, differences in mate quality—and, therefore, selective pressures in favor of mate choice—are probably common. In females, the number of eggs remaining to be laid (and therefore, their value for males) can vary widely depending on the number of eggs already laid and on female size (Parlange, 1991; Cordero, 1996). In the laboratory, females mate a second time until they have laid a substantial proportion of their eggs (Cordero, 1996). In males, the quantity of nutritious ejaculate transferred to females varies with the size and mating history of the male (Cordero, 1996); besides, for a female to be the second male's mate of the day means not only a small ejaculate, but also a lengthy copulation (> 5 h *vs.* 30.3 minutes).

Given the common occurrence of unsuccessful courtships (56.5 % of 23 courtships observed in 1989, and 85.3 % of 34 observed in 1990), mate choice prior to copulation probably exists in *C. xami*. However, a detailed study remains to be conducted. "Copula interruption" suggests mate choice after mating began. However, it is not possible to tell with the available information whether female or male choice is responsible for this behavior. Females or males may be able to evaluate their mating partners after copulation begins and decide to interrupt it within a few minutes (Eberhard, 1985, 1994, *in press*; Eberhard and Cordero, 1995; Cordero, 1995). The fact that females are the behaviorally "active" sex during the process of separation cannot be

used as evidence of female choice, given that for females it may be convenient to interrupt mating with a male that, although desirable, is unwilling (because of mate choice reasons) to transfer an ejaculate. It is also conceivable that the male manipulates (chemically or mechanically) the female, inducing her to finish copulation against her own interests. However, the fact that in the case of 1989 the male found the female again, less than three minutes after separation, and unsuccessfully courted her for a second time, suggests that female choice is involved in at least some of the post-coupling "rejections". The fact that copula interruption occurs a few minutes after genital coupling begin may be due to rapid assessment of mate quality or to the fact that as time advances it may be physically difficult to interrupt copulation (Wickman, 1985).

Acknowledgments. I thank Dr. César Domínguez, Dr. Constantino Macías, Dr. Juan Núñez, and two anonymous reviewers for helpful comments that greatly improved the manuscript. Gabriela Jiménez helped me to observe butterflies. During the course of this work I was supported by a Consejo Nacional de Ciencia y Tecnología (México) scholarship.

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